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# Evaluation of a modified reciprocal recurrent selection procedure for maize improvement

## Abstract

Reciprocal recurrent selection in maize (*Zea mays* L.) has been very successful in improving yields of crosses of two populations wherein each population has been used as a tester for the other. A modification of the procedure was suggested that uses two inbred lines as testers instead of the populations. The purpose of our research was to compare the two procedures for progress achieved after three cycles of recurrent selection. The populations were BS21 and BS22 Synthetics used in a reciprocal recurrent selection program (BS21R x BS22R). For the modified procedure, inbred A632 was the tester for BS21, [BS21(A632HI)]; and inbred H99, for BS22, [BS22(H99HI)]. Progress was evaluated in six crosses: BS21(R) x BS22(R), BS21(A632HI) x A632, BS22(H99HI) x H99, BS21(R) x A632, BS22(R) x H99, and BS21(A632HI) x BS22(H99HI). Grain yield showed highly significant  $P < 0.01$  linear gains for BS21(R) x BS22(R) (4.9% cycle), BS21(A632HI) x A632 (3.6 cycle), and BS21(R) x A632 (4.7%/cycle); gains for the other crosses were positive, but not significant. Evidently, after three cycles of selection, the modified procedure was not successful in improving yield for crosses of the populations. The results indicated that choice of inbred testers may be very critical in the modified procedure. Grain moisture had highly significant linear decreases for BS21(A632HI) x A632, BS22(R) x H99, and BS21(A632HI) x BS22(H99HI). Highly significant changes were observed for lodging as follows: root lodging decreased for BS21(A632HI) x A632 and BS21(R) x A632; stalk lodging decreased for BS21(R) x BS22(R) and BS21(R) x A632, but increased for BS21(A632HI) x BS22(H99HI).

## Keywords

Corn, Reciprocal recurrent selection, Maize synthetics, Grain yield

## Disciplines

Agricultural Science | Agronomy and Crop Sciences | Plant Breeding and Genetics

## Comments

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# EVALUATION OF A MODIFIED RECIPROCAL RECURRENT SELECTION PROCEDURE FOR MAIZE IMPROVEMENT\*<sup>1</sup>

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**ABSTRACT** - Reciprocal recurrent selection in maize (*Zea mays* L.) has been very successful in improving yields of crosses of two populations wherein each population has been used as a tester for the other. A modification of the procedure was suggested that uses two inbred lines as testers instead of the populations. The purpose of our research was to compare the two procedures for progress achieved after three cycles of recurrent selection. The populations were BS21 and BS22 Synthetics used in a reciprocal recurrent selection program (BS21R x BS22R). For the modified procedure, inbred A632 was the tester for BS21, [BS21(A632HI)]; and inbred H99, for BS22, [BS22(H99HI)]. Progress was evaluated in six crosses: BS21(R) x BS22(R), BS21(A632HI) x A632, BS22(H99HI) x H99, BS21(R) x A632, BS22(R) x H99, and BS21(A632HI) x BS22(H99HI). Grain yield showed highly significant ( $P < 0.01$ ) linear gains for BS21(R) x BS22(R) (4.9%/cycle), BS21 (A632HI) x A632 (3.6%/cycle), and BS21(R) x A632 (4.7%/cycle); gains for the other crosses were positive, but not significant. Evidently, after three cycles of selection, the modified procedure was not successful in improving yield for crosses of the populations. The results indicated that choice of inbred testers may be very critical in the modified procedure. Grain moisture had highly significant linear decreases for BS21(A632HI) x A632, BS22(R) x H99, and BS21(A632HI) x BS22(H99HI). Highly significant changes were observed for lodging as follows: root lodging decreased for BS21(A632HI) x A632 and BS21(R) x A632; stalk lodging decreased for BS21(R) x BS22(R) and BS21(R) x A632, but increased for BS21(A632HI) x BS22(H99HI).

**KEY WORDS:** Corn; Reciprocal recurrent selection; Maize synthetics; Grain yield.

## INTRODUCTION

The primary goal of maize breeders (*Zea mays* L.) is the development of inbred lines that have superior agronomic performance in single-cross hybrids. The most important agronomic traits are grain yield, maturity, resistance to root and stalk lodging, resistance to diseases and insects, and grain quality. Planned crosses, commonly single-cross or back-cross populations in which the component parents are usually elite lines, have been the primary breeding sources (BAUMAN, 1981). Synthetic maize populations, narrow and broad genetic base, have also been used as breeding sources. Synthetic populations, however, are not used extensively, primarily because average frequencies for favorable alleles, or combinations of favorable alleles to give above-average genotypes, seem less than those for planned crosses. Maize synthetics are amenable to improvement, which should make them better source populations for applied breeding programs.

Recurrent selection is a cyclical breeding procedure designed to improve a population gradually for a certain trait, or traits, while maintaining genetic variability to assure continued opportunity for improvement. Several recurrent selection procedures have been used successfully in maize to improve several agronomic traits. Additive genetic effects are utilized in all types of recurrent selection, whereas other types were designed to give more emphasis to nonadditive genetic effects. JENKINS (1940) proposed a recurrent selection procedure for general combining ability wherein the basis of evaluation is testcross performance with a heterogeneous tester; thus, selection is primarily for additive gene effects. HULL (1945) suggested a modification that uses an inbred line as tester and was intended to select for specific combining ability with the tester. Hull believed that overdominance was the primary type of gene action in

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hybrid maize, and his procedure emphasized selection for nonadditive genetic effects. COMSTOCK *et al.* (1949) outlined the reciprocal recurrent selection procedure in which two broad-based populations are used reciprocally as sources and testers. The method was designed to improve the interpopulation cross of the two source populations and was expected to be successful regardless of the type of gene action. Several recurrent selection methods have been used successfully to effect population improvement in maize (HALLAUER and MIRANDA, 1988).

RUSSELL and EBERHART (1975) suggested a modified reciprocal recurrent selection procedure in which the testers are two inbred lines. Two populations, A and B, should be selected opposite one another in a heterotic pattern and should show a strong indication of hybrid vigor when crossed. The tester for population A should be an inbred line unrelated to A, but may be related to B; likewise, the tester for population B should be an inbred line unrelated to B, but may be related to A. By using an inbred line tester, the problem of sampling in a heterogeneous tester is removed. Also, if the testers are elite lines being used in hybrid seed program, superior germplasm identified from A and B can be moved into a breeding nursery for the development of new inbred lines. Based on several studies that have used inbred testers in recurrent selection, it seemed that improvement was a result of increasing alleles with relatively large additive effects (RUSSELL *et al.*, 1973; WALEJKO and RUSSELL, 1977; HORNER *et al.*, 1989).

A program to evaluate the modified reciprocal recurrent selection procedure was initiated in the maize breeding program at Iowa State University in 1975. The objective of the present study is to compare gain for recurrent selection procedures using inbred line and reciprocal populations as testers.

## MATERIALS AND METHODS

The materials for this study were two maize synthetics, BS21 and BS22, whose approximate maturities are AFS500. BS21 was formed by intermating two synthetics, BS5, and BS20; 23 lines were intermated to form BS5 (EBERHART *et al.*, 1972) and 12 lines were intermated to form BS20 (RUSSELL *et al.*, 1976). BS22 was formed by intermating 16 inbred lines. Because one inbred line and some Iowa Stiff Stalk Synthetic (BS5S) germplasm are common to BS21 and BS22, the two synthetics are genetically related. The estimated relationship, however, is less than 1%.

BS21 and BS22 were used in both a reciprocal recurrent selection program and a modified reciprocal recurrent selection procedure. BS21(R)Cn and BS22(R)Cn were used reciprocally (COMSTOCK *et al.*, 1949). For the modified reciprocal recurrent selection pro-

gram, inbred line A632, remotely related to BS22, was used to test  $S_0$  plants of BS21(A632H)Cn; and inbred line H99, remotely related to BS21, was used to test  $S_0$  plants of BS22(H99H)Cn. When the program was initiated, the single cross, A632 x H99, was an elite cross in its maturity group (AES600). The breeding materials were divided into three groups – BS21(A632H), BS22(H99H), and BS21(R) and BS22(R) – to distribute the work load. Each group was handled in separate years with respect to formation of testcross families, evaluation, recombination of selected lines, and random mating. Recombination was achieved by a bulk diallel (STUBER, 1980) followed by one generation of random mating in a winter nursery. Thus, each cycle required four generations (three years) to complete.

Most cycles had about 200 to 220 testcrosses for evaluation and 20 to 22  $S_1$  selected lines (seed from a plant that was selfed and testcrossed to form progeny for evaluation) were recombined. The testcrosses were evaluated for one year at three locations in northern Iowa, two replications at each location. Conventional two-row plots, 5.18 cm x 0.76 cm, were used. Planting and harvesting were done by machinery adapted for small plot work. Selection of  $S_1$  lines for recombination was based on yield, moisture, root lodging, and stalk lodging of testcross progeny. Three cycles were completed; thus, for this study we had available the C0, C1, C2, and C3 populations from BS21(A632H), BS22(H99H), BS21(R), and BS22(R).

During the recurrent selection cycles, testcrosses for BS21(R) and BS22(R) were grown in the same season. Testcrosses for BS21(A632H) and BS22(H99H) were grown in different seasons and in different seasons from BS21(R) and BS22(R), except that in the third cycle testcrosses of BS21(R), BS22(R), and BS21(A632H) were grown in the same season. Thus, differences among variance component estimates, repeatability values, and selection differentials (Table 1) may have been caused partly by seasonal differences as well as genetic differences.

Predicted gains for grain yield (Table 2) were similar for BS21(A632H), BS21(R), and BS22(R), but were consistently lower for BS22(H99H). Selection differentials for yield were similar among all sets of testcrosses, but the BS22(H99H) testcrosses generally had lower repeatability values (Table 1). Only slight changes were expected in grain moisture (Table 2) because selection was to retain average moisture. Good predicted gains were indicated for resistance to both root and stalk lodging; however, actual lodging values (data not shown) showed greater gains were expected for root lodging than for stalk lodging.

The materials used in this evaluation included Cycles 0 to 3 of the following crosses: BS21(R) x BS22(R), BS21(A632H) x BS22(H99H), BS21(A632H) x A632, BS21(R) x A632, BS22(H99H) x H99, and BS22(R) x H99 (Table 3). Thus, with duplicate entries for C0 x C0 and C0 x inbred tester crosses, there were 24 crosses as entries for evaluation. The population crosses were produced in paired rows by using at least 100 plants from each heterogeneous source. Every plant was sampled once, as a male or female, to minimize confounding effects by sampling differences in heterogeneous materials. A more comprehensive evaluation, which included the populations *per se* and more testers, was reported by BLACKBURN (1989); that study, however, did not include BS21(A632H)Cn x BS22(H99H)Cn.

Evaluation trials included four single-cross hybrids that have slightly later anthesis than BS21 and BS22. The single crosses were included to have a performance level for adapted materials; they are not a part of the evaluation. Evaluation trials were planted at three widely separated northern Iowa locations – Sutherland,

TABLE 1 - Variance components estimates, repeatability values, and selection differentials for yield in each cycle of selection in BS21(A632IH), BS22(H99IH), BS21(R), and BS22(R).

Population		Variance component estimates			Repeatability	Selection differential
		$\hat{\sigma}_T^2$	$\hat{\sigma}_{gT}^2$	$\hat{\sigma}_g^2$		
						q/ha
BS21(A632HI)	1	129.42	0.65	36.14**	0.62	11.3
	2	69.97	5.01	23.38**	0.64	6.9
	3	45.82	5.39**	10.05**	0.52	6.2
BS22(H99IHI)	1	57.75	1.14	16.49**	0.52	7.0
	2	66.17	8.68*	15.56**	0.43	7.6
	3	70.40	0.00	12.20**	0.51	8.0
BS21(R)	1	80.62	1.94	28.33**	0.67	8.2
	2	100.25	1.72	25.38**	0.80	7.6
	3	53.71	2.54	12.04**	0.55	6.2
BS22(R)	1	79.58	2.24	24.93**	0.64	8.6
	2	87.97	4.98	22.32**	0.78	7.3
	3	51.20	4.43	16.22**	0.62	7.7

\*, \*\* Mean square values significant at P = 0.05 and 0.01, respectively.

TABLE 2 - Number of lines tested, number of lines selected, and predicted testcross gains for each cycle of selection in BS21(A632IH), BS22(H99IH), BS21(R), and BS22(R).

Population	Cycle of selection	Number of lines tested	Number of lines selected	Predicted gains <sup>‡</sup>			
				Yield	Moisture	Root lodging	Stalk lodging
BS21(A632IH)	1	219	20	11.0	1.0	— <sup>‡</sup>	—18.3
	2	217	22	5.8	0.0	—26.6	—18.7
	3	219	22	7.4	0.0	—20.9	—6.9
BS22(H99HI)	1	204	20	4.6	—2.2	—18.9	— <sup>‡</sup>
	2	197	20	4.1	1.0	—9.9	—6.6
	3	221	22	4.4	0.0	—15.0	—8.9
BS21(R)	1	176	20	8.8	0.0	—12.8	—27.7
	2	208	21	9.7	0.0	—20.7	—1.2
	3	206	22	7.1	0.0	0.0	—18.8
BS22(R)	1	190	20	8.0	0.0	—26.3	—25.3
	2	208	21	8.9	0.0	—18.7	0.0
	3	221	22	10.0	1.4	—9.1	—20.9
BS21(R)Cn x BS22(R)Cn <sup>§</sup>	1	—	—	8.4	0.0	—19.6	—26.5
	2	—	—	8.3	0.0	—19.7	—0.6
	3	—	—	8.6	1.2	—4.6	—19.8

<sup>‡</sup> (Mean of selected testcrosses - mean of all testcrosses) x Repeatability, expressed in percentage of mean of all testcrosses.<sup>‡</sup> No expression for trait.<sup>§</sup> Average of BS21(R) and BS22(R).

TABLE 3 - Grain yield, moisture, root lodging, and stalk lodging for four cycles of crosses for BS21 and BS22.

Cross	Recurrent selection cycles				b <sub>0</sub>	b <sub>I</sub>
	C0	C1	C2	C3		
Grain yield (q/ha)						
BS21(R) x BS22(R)	46.6	50.4	50.7	53.4	46.7	2.28 ± 0.70**
BS21(A632HI) x BS22(H99HI)	46.6	46.4	47.4	48.7	46.7	0.51 ± 0.70
BS21(A632HI) x A632	47.6	45.3	52.1	50.6	46.2	1.75 ± 0.70**
BS21(R) x A632	47.6	45.5	51.4	53.5	46.2	2.24 ± 0.70**
BS22(H99HI) x H99	55.1	54.9	57.0	56.4	55.1	0.56 ± 0.70
BS22(R) x H99	55.1	54.2	57.7	54.3	55.1	0.14 ± 0.70
LSD (0.05) = 5.1						
Average - 4 single crosses = 64.0						
Grain moisture (%)						
BS21(R) x BS22(R)	20.6	19.7	19.9	20.1	20.4	-0.18 ± 0.16
BS21(A632HI) x BS22(H99HI)	20.6	19.5	20.1	19.0	20.4	-0.40 ± 0.16**
BS21(A632HI) x A632	18.7	17.5	18.1	17.5	18.7	-0.44 ± 0.16**
BS21(R) x A632	18.7	19.4	19.8	19.1	18.7	0.28 ± 0.16
BS22(H99HI) x H99	22.4	22.1	22.1	22.0	22.4	-0.14 ± 0.16
BS22(R) x H99	22.4	21.9	20.2	19.8	22.4	-0.89 ± 0.16**
LSD (0.05) = 1.2						
Average - 4 single crosses = 20.4						
Root lodging (%)						
BS21(R) x BS22(R)	5.3	4.2	2.1	2.4	5.3	-1.17 ± 0.60
BS21(A632HI) x BS22(H99HI)	5.3	5.4	4.4	3.8	5.3	-0.46 ± 0.60
BS21(A632HI) x A632	8.0	4.7	4.0	4.3	7.5	-1.39 ± 0.60**
BS21(R) x A632	8.0	6.4	4.7	3.7	7.5	-1.28 ± 0.60**
BS22(H99HI) x H99	1.3	0.6	1.9	3.0	1.3	0.40 ± 0.60
BS22(R) x H99	1.3	2.4	2.1	1.0	1.3	0.12 ± 0.60
LSD (0.05) = 4.6						
Average - 4 single crosses = 1.8						
Stalk lodging (%)						
BS21(R) x BS22(R)	15.6	13.4	10.0	6.8	16.0	-3.03 ± 0.72**
BS21(A632HI) x BS22(H99HI)	15.6	16.6	24.6	19.9	16.0	2.10 ± 0.72**
BS21(A632HI) x A632	15.1	18.2	16.7	15.8	15.5	0.44 ± 0.72
BS21(R) x A632	15.1	11.1	11.7	7.9	15.5	-2.47 ± 0.72**
BS22(H99HI) x H99	10.2	10.6	11.2	10.6	10.0	0.10 ± 0.72
BS22(R) x H99	10.2	10.5	7.9	7.0	10.0	-1.13 ± 0.72
LSD (0.05) = 5.5						
Average - 4 single crosses = 5.6						

\*\* Highly significant ( $P = 0.01$ ).

Kanawha, and Nashua, in 1988 and 1989. These are the same locations used during the three cycles of selection when testcrosses were evaluated. Conventional two-row plots, 5.18 x 0.76 cm, were planted and harvested by small plot machinery. Plots were overplanted and thinned at the 5- to 6-leaf stage to give densities of 62000 plants/ha in 1988 and 56000 plants/ha in 1989. In 1989, the 28 entries were part of a larger trial with a triple lattice design including the populations per se and more sets of testcrosses. The field design in 1989 was a randomized complete block with three replications at each location. All field areas had fertilizer applications to promote high yields, and weed control was achieved by herbicide application and field cultivation. Data were taken for the following traits: grain yield (converted to q/ha at 15.5% moisture)

and percentages of grain moisture, root lodging, and stalk lodging. There was no gleaned for ears on the ground at harvest.

**Statistical Analyses:** The 1988 trials were evaluated by using a 10 x 10 triple lattice. The data for each trial were analyzed separately to obtain entry means adjusted for block effects according to the lattice design. Mean values for the 28 entries in each location were used along with mean values from the three 1989 trials to obtain combined analyses of variance for grain yield, grain moisture, and stalk lodging. The Nashua location in 1988 and 1989 and the Kanawha location in 1988 were not included in the combined analyses of variance for root lodging because the trait was not expressed in these environments. In the combined analyses, entries were considered fixed effects, and each year-location com-



bination was considered a random environment which gave rise to entries  $\times$  environments sums of squares for each trait. Pooled error mean squares over six environments (three environments for root lodging) were obtained by summing the error sum of squares for each environment. Because the C0 population crosses of BS21  $\times$  A632, BS22  $\times$  H99, and BS21  $\times$  BS22 were included twice as entries in each experiment, there were only 24 degrees of freedom (df) for entries.

The 24 df for entries were partitioned into 20 df for BS21 and BS22 testcrosses and population crosses, 3 df for checks, and 1 df for the contrast of checks vs. the remaining entries. The entries  $\times$  environments interaction was partitioned similarly. The C0, C1, C2, and C3 testcrosses were separated into three regression groups based on common C0 genotypes. For example, the BS21(R)Cn  $\times$  A632 and BS21(A632HI)Cn  $\times$  A632 testcrosses comprised one of the groups. The sums of squares for each regression group were partitioned by using the procedure of EBERHART (1964). This analysis allowed fitting both regression lines through the common C0 intercept and provided a direct test in the analysis of variance of whether the slopes of the regression lines were significantly different. Because the C0 testcrosses of each group had twice as many observations as the other cycles, weighted least squares was used where the weights were the variances of the cycle means. Standard errors of the regression coefficients were obtained by taking the squares root of the appropriate diagonal element of the  $(X'W^{-1}X)^{-1}$  matrix, where the diagonal elements of  $W$  are the variances of the cycle means and the off-diagonal elements are zero.

## RESULTS AND DISCUSSION

All environments, except Sutherland in 1989, had relatively low yields because of drought. Sutherland in 1989 had yields near average for this location. Stalk lodging at all locations in 1988 and at Sutherland and Kanawha in 1989 was probably great enough to cause some harvest losses, thus contributing to experimental error for yield.

Differences among entries for all traits were highly significant ( $P < 0.01$ ) in all environments and in the combined analyses over environments (ANOVA not shown). The interactions for entries  $\times$  environments were highly significant for all traits, but the sums of squares for the interactions were less than for the main effects of entries. The coefficient of variability for yield was 11.8%, which is an acceptable value for the average yield of 53.0 q/ha.

The cross of BS21(R)Cn  $\times$  BS22(R)Cn, from the reciprocal recurrent selection program, had a realized gain of 2.28 q/ha/cycle (4.9%/cycle, Table 3). The gains occurred in the first and third cycles. The average predicted gain from the selection cycles was 8.5%/cycle for BS21(R) and 9.0% for BS22(R) (Table 2). For BS21(A632HI)Cn  $\times$  A632, the realized gain was 1.73 q/ha/cycle (3.6%/cycle), whereas the average predicted gain was 8.1%/cycle. Cycles 1 and 3

showed yield decreases from cycles 0 and 2, respectively, indicating a nonsignificant cubic trend. The average predicted gain from the selection trials was 4.4%/cycle for the cross of BS21(H99HI)Cn  $\times$  H99, which was the lowest predicted gain among the four populations, and a nonsignificant yield gain was achieved. The crosses of BS21(R)Cn  $\times$  A632 showed a highly significant gain of 2.24 q/ha/cycle (4.7%/cycle), whereas BS22(R)Cn  $\times$  H99 showed no gain. The cycle crosses for BS21(A632HI)Cn  $\times$  BS22(H99HI)Cn showed a nonsignificant gain, which was considerably less than the average realized for BS21(A632HI)Cn  $\times$  A632 and BS22(H99HI)Cn  $\times$  H99. Moreover, the yields of C2 and C3 were the lowest observed among the same cycles for other crosses.

In all evaluation trials, the realized gains were less than the predicted gains calculated during the cycles of recurrent selection. If genotype  $\times$  environment interactions ( $\sigma_{ge}^2$ ) are underestimated, or main effects of testcrosses ( $\sigma_g^2$ ) are overestimated, during recurrent selection cycles the repeatability estimates will be inflated, thus causing gains to be overestimated. During the recurrent selection cycles,  $\sigma_{gl}^2$  was significant in only two instances (Table 1), which was an unusual result for yield tests. Genotypes  $\times$  environment effects during evaluation, as in this study, will not be the same as those observed previously in the selection cycles, which causes further decreases in realized gains compared with predicted gains.

The failure to show a significant yield gain for BS22(H99HI)Cn  $\times$  H99 may have several causes. Before a significant trend becomes established, more than three cycles may be needed for certain sources when an elite inbred-line tester is used. This possibility was suggested in earlier studies of a long-term, half-sib recurrent selection program in Iowa Stiff Stalk Synthetic for which no gains were observed at C3 (PENNY *et al.*, 1963), but for which highly significant, linear gains were found at C7 (HALLAUER *et al.*, 1983). Sampling in a heterogenous source may not be adequate when seed is prepared for an evaluation experiment. This is suggested when comparisons have been made of the same materials in different evaluation experiments (PENNY *et al.*, 1963; HALLAUER *et al.*, 1983). For this study, we used 100 plants of BS22(H99HI) in each cycle to produce the crosses, but this may not have been adequate, particularly because some assortative mating could have occurred as a result of variation in time of anthesis and silk emergence. Further sampling is involved when seed is processed and prepared for planting. Some data from a more extensive evaluation of these materials

by Blackburn (1989) suggest that sampling may have been involved. Crosses of BS22(H99HI)Cn with three other testers (inbred A239, BS21C0, and BS22C0) showed significant increases with A239 and BS22C0; and averaged over all testers, including H99, the gain was highly significant.

When used a tester, inbred H99 may have masking effects caused by dominant, favorable alleles. During the three recurrent selection cycles, the average genetic variance component ( $\sigma_g^2$ ) for test-cross yields (Table 1) was less for BS22(H99HI) than for BS22(A632HI), and considerably less than for BS21(R) and BS22(R). COMSTOCK (1979) showed that an elite inbred-line tester may cause this problem. The predicted gain in each cycle of BS22(H99HI) was about 50% of the predicted gain for the other three populations (Table 2).

The crosses of BS21(A632HI) x BS22(H99HI) had a realized gain of 0.51 q/ha/cycle, which was not significant (Table 3). WALEJKO and RUSSELL (1977) found that Alph C5 x Lancaster C5 yielded 41.2% more than Alph C0 x Lancaster C0; inbred line B14 was the tester for Alph and inbred line Hy for Lancaster. Alph C5 x B14 yielded 11.8% more than Alph C0 x B14 (2.4%/cycle); Lancaster C5 x Hy yielded 13.1% more than Lancaster C0 x Hy (2.6%/cycle). Probably, Alph C0 and Lancaster C0 have lower gene frequencies for favorable alleles affecting yield than BS21C0 and BS22C0 do. RUSSELL and EBERHART (1975) based their recommendation of the modified reciprocal recurrent selection procedure on the inbred tester giving a greater genetic variance among testcross families than if a population is the tester (HORNER *et al.*, 1973; DARRAH *et al.*, 1972). Based on theoretical considerations, COMSTOCK (1979) concluded that the average rate of change in allelic frequencies in both populations of a reciprocal recurrent selection program will not be more rapid with the inbred tester procedure. He argued that a population tester would tend to be more likely to have the appropriate gene frequencies to assure progress than the elite inbred testers would.

If an inbred tester results in population improvement primarily because of selection for additive effects, as suggested by earlier studies (RUSSELL *et al.*, 1973; HORNER *et al.*, 1973; WALEJKO and RUSSELL, 1977), then the gain should be evident in a cross such as BS21(A632HI)Cn x BS22(H99HI)Cn. Evidently, the lack of significant gain for BS22(H99HI) offsets the significant gain for BS21(A632HI), and complementary improvement between the two populations did not occur. It seems doubtful that drought

had an effect on the observed results. BLACKBURN (1989) found that observed gain for BS21(R)Cn x BS22(R)Cn was essentially the same in a non-drought year, 1987, as in a drought year, 1988. In this study, the Sutherland location in 1989 did not experience drought conditions, yet BS21(A632HI)Cn x BS22(H99HI)Cn did not show a significant trend for yield gain in this environment.

Grain moisture showed significant, negative trends for three crosses, nonsignificant, negative trends for two crosses, and a nonsignificant, positive trend for one cross (Table 2). BLACKBURN (1989) found negative trends for all crosses except BS22(H99HI)Cn x H99 in terms of days to anthesis and days to silk emergence. All populations *per se* had highly significant, negative trends for days to anthesis and silk emergence. The  $S_1$  lines used for recombination were selected to avoid change in maturity due to grain moisture at harvest (Table 1). There may have been selection for earliness when the testcrosses were made because there is a strong tendency at pollination to begin as the first plants become available and later flowering plants of the populations are not used. Also, all populations *per se* and all crosses had highly significant, negative linear trends for ear height except BS22(H99HI) x H99, which had a nonsignificant, negative trend (BLACKBURN, 1989). It seems that the populations became earlier and shorter, which suggests a decrease in vigor. A decrease in vigor is usually negatively associated with yield gain, and is likely a factor in the lower than predicted realized gains.

When conditions permitted during the selection phase of the program, resistance to root and stalk lodging was a part of the selection. Thus, in all instances except two (Table 2), there was selection for lodging resistance although the selection differentials (data not shown) were too small to be of any consequence in two cycles. Lodging data (Table 3) show that improvement for lodging resistance was achieved for BS21(R)Cn x BS22(R)Cn and BS21(A632HI)Cn x A632, but not for BS22(H99HI)Cn x H99. Inbred H99 contributes good resistance for root and stalk lodging to hybrids; consequently, H99 probably had a masking effect on the expression of resistance in the cycles when BS22(H99HI)Cn testcrosses were selected and also on the materials with which it was crossed for this study. Precision in the expression of root and stalk lodging in standard yield trials is generally poor, and additional cycles and considerably more replications are required to establish definite trends.



With the completion of three cycles of recurrent selection, it seems that the use of A632 and H99 inbred lines, rather than the populations, as testers has not achieved gains in crosses of BS21(A632HD)Cn and BS22(H99HD)Cn. The half of the program using H99 as the tester did not have a significant yield gain by C3 and, in crosses of the two populations, may have masked gains achieved with the A632 tester. This may indicate a poor choice of tester, which unfortunately does not become evident for several cycles. These inbred lines were used as testers, however, because a second purpose was to identify  $S_1$  lines that could be moved into an applied breeding program. Inbreds A632 and H99, at the time the recurrent selection program was initiated, were representative of elite germplasm of their maturity being used in applied breeding and seed production. WALEJKO and RUSSELL (1977) also found that gains realized by recurrent selection after five cycles in two populations, Lancaster and Kolkmeier, with inbred tester Hy were not expressed when evaluated in testcrosses to inbred line B73, which is unrelated to the populations and inbred line Hy. Our present recurrent selection program has been continued, with selection for longer season maturity based on later silk emergence in the populations *per se* and grain moisture at harvest. When additional cycles of selection have been completed, which is expected to occur in the 1993 season, another evaluation will be made.

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